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LETTER

Carryover effects from natal habitat type upon competitive ability lead to trait divergence or source–sink dynamics

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Abstract

Local adaptation to rare habitats is difficult due to gene flow, but can occur if the habitat has higher productivity. Differences in offspring phenotypes have attracted little attention in this context. We model a scenario where the rarer habitat improves offspring's later competitive ability – a carryover effect that operates on top of local adaptation to one or the other habitat type. Assuming localised dispersal, so the offspring tend to settle in similar habitat to the natal type, the superior competitive ability of offspring remaining in the rarer habitat hampers immigration from the majority habitat. This initiates a positive feedback between local adaptation and trait divergence, which can thereafter be reinforced by coevolution with dispersal traits that match ecotype to habitat type. Rarity strengthens selection on dispersal traits and promotes linkage disequilibrium between locally adapted traits and ecotype-habitat matching dispersal. We propose that carryover effects may initiate isolation by ecology.

Keywords

Developmental effects, ecological speciation, epigenetics, habitat selection, maternal effects, natal effects, natal-habitat preference induction, silver spoon, source–sink, spatial genetic variation.

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INTRODUCTION

What allows a population in a heterogeneous landscape to become locally adapted? One well-studied consideration is a tug-of-war between divergent selection and the homogenising effects of gene flow (Hendry *et al*. 2002). Local adaptation to different habitat types (leading to locally adapted ecotypes) can be due to very strong selection (e.g. Hoekstra *et al*. 2004; Richardson & Urban 2013) and gene flow barriers during dispersal (e.g. Edelaar *et al*. 2008; Arnoux *et al*. 2014; Richardson *et al*. 2014; Adams *et al*. 2016) or at the reproductive stage (e.g. Wood & Keese 1990; Filchak *et al*. 2000; Hendry & Day 2005; Friesen *et al*. 2007; Thomas 2013).

Another consideration is the balance between habitat frequency vs. quality (Kawecki 1995). In a well-mixed population, selection pressure is proportional to how many individuals encounter each habitat type, thus natural selection will favour adaptation to common habitats (Kawecki & Stearns 1993; Kawecki 1995). However, selection also favours adaptation to a high-quality habitat type that offers a higher per-capita growth rate; first, because the flow of genes from high-quality to low-quality habitat will swamp genes locally adapted to the latter, and second, because the low-quality habitat contributes less to the future gene pool (Holt & Gaines 1992). Therefore selection can favour adaptation to the minority habitat type if it has high enough quality to overcome its relative rarity in the landscape (Kawecki 1995).

Habitat quality above usually refers to the quantity of offspring produced, however an alternative aspect, which we focus on here, is the quality of the offspring. There are many examples where natal environment alters the phenotype of an individual (e.g. Cam & Aubry 2011), with fitness consequences that are carried over to the adult life-stage (Grafen 1988; Pechenik *et al*. 1998; Senner *et al*. 2015). These carryover effects (sensu O'Connor *et al*. 2014) can be initiated by the natal habitat type (Lindström 1999; Van Allen & Rudolf 2016), and can manifest as competitive and breeding advantages at the adult stage (e.g. Mumme *et al*. 2015). For example: early-life nutrition (Metcalfe & Monaghan 2001) can influence adult size (Hopwood *et al*. 2014) or other characteristics relevant to within-sex competition for territory and mates (Spencer *et al*. 2004; Wilkin & Sheldon 2009; Grava *et al*. 2012); local habitat factors can improve propagule quality (Stanton *et al*. 1997); and early resource timing may provide a competitive advantage to young adults (Johansson *et al*. 2014) in cases where there is a prior residence effect (Braddock 1949; Kokko *et al*. 2006).

The relative impact of habitat frequencies vs. carryover effects is analogous to the better known contrast between frequencies and per-capita growth rates in source–sink studies (e.g. Kawecki 1995). A habitat with higher quality, by merit of producing more-competitive offspring, will make a greater contribution to the gene pool, creating a genetic source-sink dynamic analogous to the ecological source-sinks discussed above (c.f. Reid *et al*. 2006). Asymmetric gene flow from high-

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to low-quality habitat may counteract adaptation to the low-quality habitat type (c.f. Stanton *et al.* 1997) if high-quality habitat is relatively common in the landscape; if it is rare, local adaptation to the low-quality habitat type may also occur.

All these results depend on dispersal, which will influence gene flow and hence the pattern of spatial genetic variation and ecological dynamics. We are interested in dispersal that coevolves with local adaptation in the presence of carryover effects. We track mathematically the following intuition. If dispersal is limited, competitively superior individuals accumulate in the high-quality habitat, forming a competitive barrier to immigrants from nearby low-quality habitat. Assuming highly competitive adults have a greater chance of winning a high-quality breeding territory and raising their offspring there (c.f. Stamps 2006), a positive feedback emerges that will promote a lineage's repeated encounters with the high-quality habitat type (e.g. Van De Pol *et al.* 2006; Grava *et al.* 2012, 2013a), which in turn may promote selection to adapt to this habitat type. Once trait divergence is initiated, dispersing to a habitat that an individual is poorly adapted to is selected against (Remeš 2000).

However, it is not straightforward to predict the evolutionary outcomes when natal habitat type, individual phenotype, and dispersal trait are all interrelated (e.g. Tarwater & Beissinger 2012). Since it is difficult to predict the outcome based upon verbal models alone, we model the evolving associations in an individual-based, genetically and spatially explicit model of a single population on a landscape consisting of two habitat types. The two habitats differ in (1) frequencies (i.e. they are not equally abundant), (2) the carryover effects on offspring's competitive ability; and (3) in other characteristics that influence an individual's reproductive success, to which individuals may be adapted or maladapted. Individuals are faced with a trade-off between adapting to one habitat type or the other, and we explore scenarios where dispersal distance and habitat preference may coevolve. We are particularly interested in the conditions that lead to trait divergence – the emergence of two distinct and locally-adapted ecotypes – that are maintained in the face of gene flow across space and sustained in time.

MODEL

The individual-based model involves reproduction, dispersal and competition (Fig. 1a) on a one-dimensional (ring) landscape of discrete breeding territories (Fig. 1b,c). Each territory represents one of two habitat types, and territories with the same habitat type are clustered in space.

Individuals are outcrossing hermaphrodites that form breeding pairs on territories, and have an evolvable trait that determines their local adaptedness. This trait determines number of offspring raised, and since an individual cannot be locally adapted to both habitat types, high reproduction in one habitat type implies low reproduction in the other. To be able to include carryover effects (the focus of our model), an individual's natal habitat type is assumed to determine its ability to compete for breeding territories. This effect operates regardless of the individual's genotype and the habitat type in which the competitive interaction takes place. One habitat type confers high competitive ability (HC) and the other low competitive ability (LC) to individuals born there.

A deterministic adaptive dynamics (Geritz *et al.* 1999; Brännström *et al.* 2013) analogue of the simulation model is included in Supplement S2 for comparison.

Individuals, their genes, and their traits

Over its lifetime, each individual i will have associated with it: a natal territory x_i, a potential breeding territory y_i upon which it settles and competes for ownership, and a genotype where several two-allelic loci additively impact a trait. All versions of our model have the reproductive trait, $\boldsymbol{\pi}_{i,r}$ (which determines local adaptedness), formed as a the sum over n_r haploid loci where each allele can take the value 0 or 1; in some versions of the model dispersal is also allowed to evolve (details below).

For all modelled traits k, the trait values increase linearly with the number of '1' alleles, and we compute the raw k-trait value $\phi_{i,k}$ for individual i with genotype $\boldsymbol{\pi}_{i,k}$ as

$$\phi_{i,k} = \phi_{k,\min} + \frac{\mathrm{sum}(\boldsymbol{\pi}_{i,k})(\phi_{k,\max} - \phi_{k,\min})}{n_k}, \quad (1)$$

where $\phi_{k,\min}$ and $\phi_{k,\max}$ determine the range of possible trait values for trait k. Raw trait values are converted into meaningful values – e.g. dispersal distances, habitat-type preferences – in different ways depending upon the trait type (below).

The landscape

The population inhabits a ring of N discrete territories, indexed 0, 1, …, $N - 1$; each territory can host only one breeding pair. Territories differ in quality: they are either HC habitats that induce high competitive ability in offspring born there, or LC habitats that induce low competitive ability. The competitive ability conferred to a juvenile i raised in natal territory x_i is modelled as a competitive weighting $w_{i,c}$ where

$$w_{i,c} = \begin{cases} c & \text{if } T_{x_i} = \mathrm{HC}, \\ 1 & \text{if } T_{x_i} = \mathrm{LC}. \end{cases} \quad (2)$$

where T_{x_i} is the habitat type of individual i's natal territory x_i, and parameter $c > 1$ quantifies the competitive advantage of individuals raised in HC.

The two habitat types also differ with respect to the optimal reproductive trait value that, when matched by the traits of the breeding pair, maximises the number of offspring produced in that habitat type. We assign territory y with habitat type T_y an optimal reproductive trait value $\hat{\phi}_r$ according to

$$\hat{\phi}_r = \begin{cases} +1 & \text{if } T_y = \mathrm{HC}, \\ -1 & \text{if } T_y = \mathrm{LC}. \end{cases} \quad (3)$$

The magnitude and sign of these values are arbitrary; all that is needed is that they are different in the different habitat types and then the strength of the trade-off between specialisation to one habitat type or the other is controlled by other parameters (below).

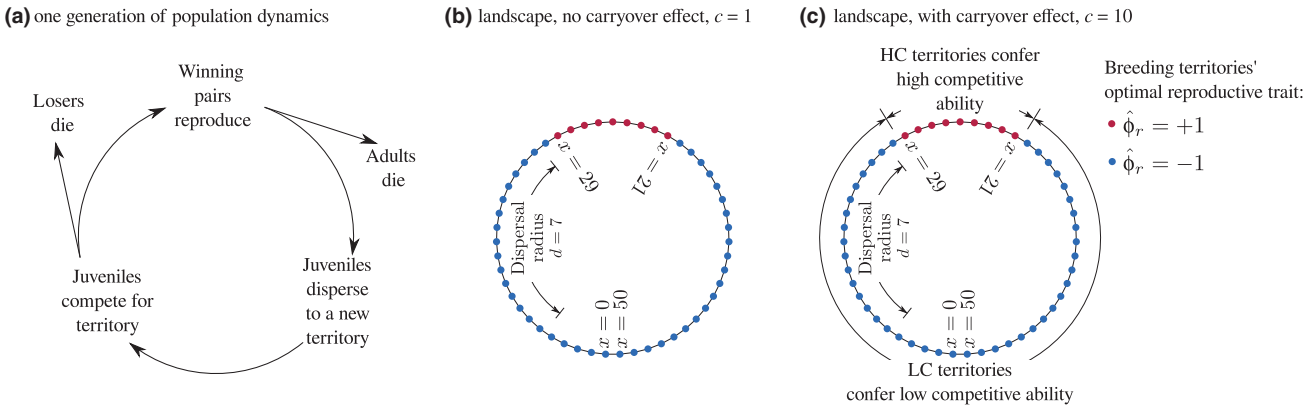

Figure 1 Population processes in the simulation model over one generation (a), and the ring of breeding territories that comprise the landscape (b–c), which can be modelled with no carryover effect (b), or with a carryover effect (c). The optimal reproductive trait $\hat{\phi}_r$ always differs between red and blue habitat types as shown. When a carryover effect is modelled, the red territories confer high competitive-ability (HC) and the blue territories confer low competitive-ability (LC) on offspring raised there. The strength of the carryover effect is determined by the parameter; $c = 10$ means that individuals raised in HC are 10 times more likely to win the competition breeding territories than individuals raised in LC.

Reproduction

Number of offspring

The number of offspring that a breeding pair produces is modelled as a Gaussian function of the difference between the breeding pairs' reproductive trait and the optimal trait in that habitat type. Individuals may specialise to one or the other habitat type, or as some compromise between the two (with a varying degree of generalism). For a territory y at year t with a breeding pair $A(y, t) = \{i, j\}$, the reproductive trait value of the pair is assumed to be the average of their individual reproductive trait values

$$\phi_{A(y,t)} = \frac{\phi_{i,r} + \phi_{j,r}}{2}. \quad (4)$$

Then the number of offspring that the breeding pair will have $r(y, t)$ is

$$r(y,t) = \text{round}\left(r_{\max}\exp\left(\frac{-(\phi_{A(y,t)} - \hat{\phi}_y)^2}{2\sigma^2}\right)\right), \quad (5)$$

where σ is a parameter controlling the strength of trade-off between adaptation to HC and LC habitats (low σ implies strong trade-off). Territories with only one solitary individual do not yield offspring.

Inheritance

Inheritance obeys free recombination, such that each offspring inherits alleles at each locus from either parent with equal independent probability. Offspring genotypes are subject to mutation: each locus has its allele mutating from 1 to 0 or vice versa with probability ε_k.

Dispersal

A juvenile surveys the neighbourhood around its natal territory, chooses one territory to be its potential breeding territory, and disperses there. All dispersal occurs simultaneously, and once a disperser has settled upon a potential breeding territory then that selection is final; therefore this model omits any direct effects of competitor density on territory preference. Different scenarios regarding dispersal trait evolution are modelled (Table 1). The radius of the neighbourhood may be fixed, or it may be determined by an evolving dispersal radius genotype $\boldsymbol{\pi}_{i,d}$. If the dispersal radius is fixed, then the potential breeding territory may be chosen at random, or it may be chosen according to an evolving habitat preference determined by genotype $\boldsymbol{\pi}_{i,h}$. Habitat preference is modelled as a random weighted choice, where weightings may either reflect a preference either for a particular habitat type (e.g. Camacho *et al.* 2013; Ousterhout *et al.* 2014), or for a habitat type matching the individual's natal habitat type (e.g. Piper *et al.* 2013) i.e. natal habitat preference induction (NHPI) (Davis & Stamps 2004).

Dispersal radius

The dispersal radius of an individual i is determined by an integer parameter d_i. In the fixed dispersal radius scenario, all individuals have $d_i = d$, otherwise d_i is calculated from the dispersal trait value by

$$d_i = \text{round}(\phi_{i,d}). \quad (6)$$

Table 1 A summary of scenarios modelled

Reproductive trait Determines local adaptedness	Dispersal trait		Scenario name	Results figures
	Dispersal radius	Habitat preference		
Evolving	Fixed	None	Evolving reproductive trait only	Fig. 2a,b, Fig. 3a,b
		By habitat type & evolving	Evolving habitat-type preference	Fig. 2c, Fig. 3c–e
		By NHPI & evolving	Evolving NHPI	Fig. 2d, Fig. 3f–h
	Evolving	None	Evolving dispersal radius	Fig. 2e, Fig. 3i–k

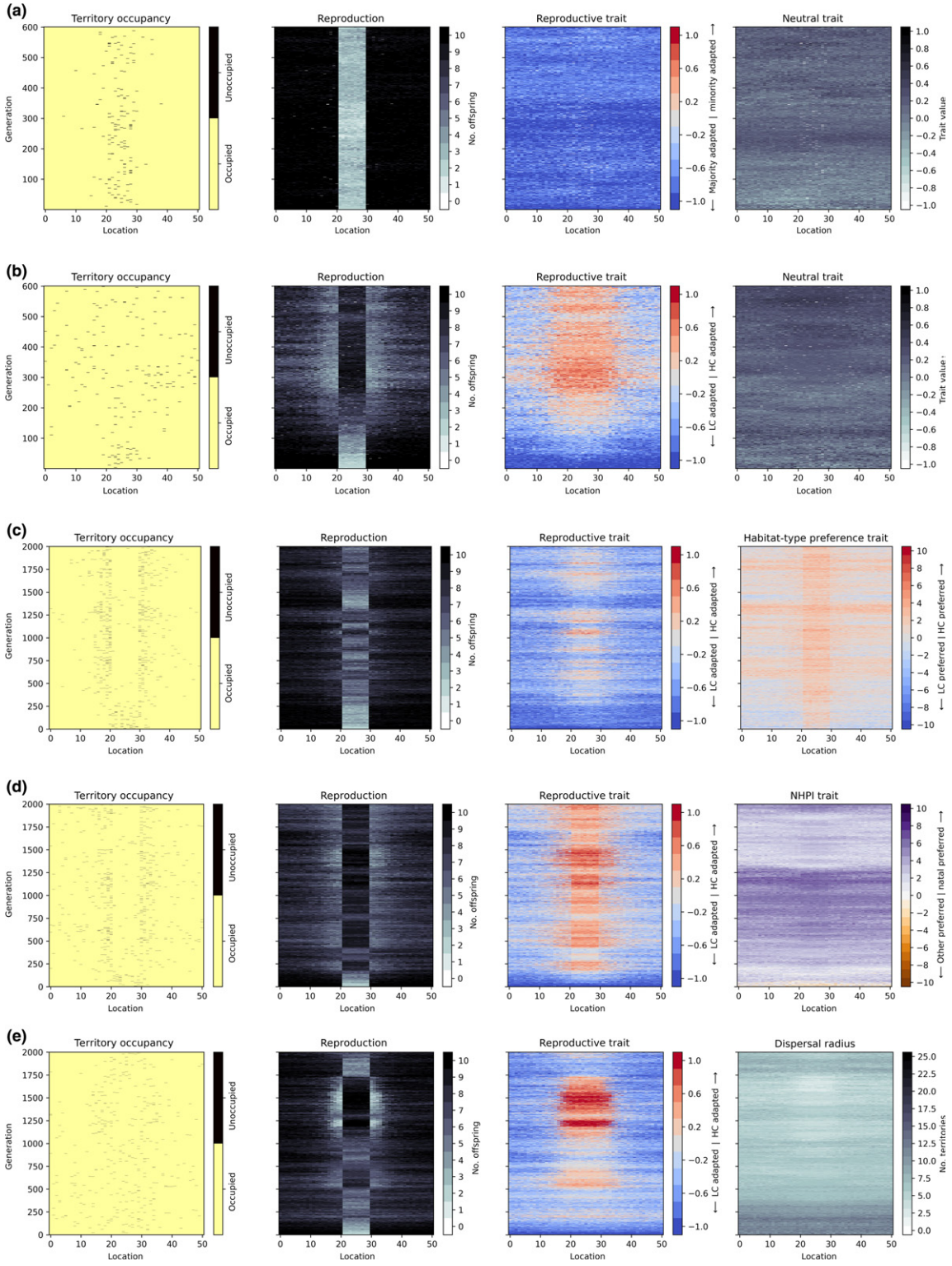

Figure 2 Representative example simulations of the ecoevolutionary dynamics in different evolutionary scenarios, showing: territory occupancy (presence of a breeding pair), reproduction (no. offspring produced), reproductive trait value, and neutral or dispersal trait value. Panel (a) is for a landscape with no carryover effect (Fig. 1b) and a scenario of evolving reproductive trait only. Panels (b–e) are for a landscape with a carryover effect ($c = 10$) such that the minority habitat type (red) confers high competitive ability on offspring (Fig. 1b). Carryover effect is coupled with scenarios of evolving: reproductive trait only (b), habitat-type preference (c), NHPI (d), and dispersal radius (e). The population was initialised with all individuals having an identical reproductive genotype that maximised reproduction in the majority habitat type (blue). In the absence of a carryover effect the population remains adapted to the majority habitat type (a), however when the minority habitat type confers high competitive ability then adaptation to both the minority and majority habitat types (red and blue) can occur (b–e). Default parameter values: $\sigma = 1.11$, $d = 7$, $r_{\max} = 10$, $n_r = n_h = n_d = 20$, $\varepsilon_r = \varepsilon_h = \varepsilon_d = 0.001$, $\phi_{r,\min} = -2$, $\phi_{r,\max} = 2$, $\phi_{h,\min} = -10$, $\phi_{h,\max} = 10$, $\phi_{d,\min} = 0$, $\phi_{d,\max} = 25$.

The individual i's dispersal neighbourhood Z_i is the set of territories from which the disperser chooses its potential breeding territory

$$Z_i = \{z : (z\text{-}x_i) \bmod N < d_i\}. \quad (7)$$

Habitat preference and weighted selection of potential breeding territory

Selection of a potential breeding territory is modelled as a random weighted choice, where the weighting $w_{i,h}(z)$ is the preference of individual i for the habitat type of territory z. The probability that disperser i chooses territory $z_j \in Z_i$ to be its potential breeding territory y_i is

$$P(y_i = z_j) = \frac{w_{i,h}(z_j)}{\sum_{z_k \in Z_i} w_{i,h}(z_k)}. \quad (8)$$

In the scenarios with no habitat preference (Table 1), all $w_{i,h}(z) = 1$. Otherwise, a disperser i will have a preferred habitat type $\hat{T}_i$, and the strength of the weighting is proportional to the preference trait

$$w_{i,h}(z) = \begin{cases} 1 + |\phi_{i,h}| & \text{if } T_z = \hat{T}_i, \\ 1 & \text{otherwise.} \end{cases} \quad (9)$$

The preferred habitat type $\hat{T}_i$ may be a fixed habitat type or may be determined by NHPI. If habitat preference is by habitat type then

$$\hat{T}_i = \begin{cases} \text{HC} & \text{if } \phi_{i,h} > 0, \\ \text{LC} & \text{otherwise.} \end{cases} \quad (10)$$

If habitat preference is by NHPI then

$$\hat{T}_i = \begin{cases} T_{x_i} & \text{if } \phi_{i,h} > 0, \\ \text{HC} & \text{if } \phi_{i,h} \leq 0 \text{ and } T_{x_i} = \text{LC}, \\ \text{LC} & \text{if } \phi_{i,h} \leq 0 \text{ and } T_{x_i} = \text{HC}. \end{cases} \quad (11)$$

Competition for breeding territory

Territories may only hold one breeding pair, and before territory competition occurs, it is assumed that all adults die. Therefore competition for each territory y at year t is between the set of juveniles $J(y, t)$ that have dispersed and settled there. Competition is modelled as random weighted choice, where the competitive weightings $w_{i,c}$ are the result of carryover effects from each individual's natal habitat type according to eqn 2. Therefore the probability that a focal individual $i \in J(y, t)$ has of becoming a member of the breeding pair on y in the next year is

$$P(i \in A(y, t+1)) = \frac{2w_{i,c}}{\sum_{k \in J(y,t)} w_{k,c}}. \quad (12)$$

It is assumed that all juveniles who lose the territory competition die.

RESULTS

Competitive carryover effect permits adaptation to high-quality minority habitat type

A carryover effect can permit adaptation to a high-quality minority habitat type and trait divergence (red and blue regions in Fig. 2b) where none would otherwise occur (blue only in Fig. 2a). In the scenario where there was no carryover effect upon competitive ability (Fig. 1b), the reproductive trait remained highly-adapted to the majority habitat type, and maladapted to the minority habitat type (Fig. 2a). Consequently, occupancy of territories and reproductive success in the minority habitat type was low, leading to source–sink ecological dynamics. In contrast, in the scenario where there was a carryover effect upon competitive ability (Fig. 1c), reproductive trait divergence occurred and two ecotypes formed in the population (Fig. 2b). Instead of source–sink dynamics, each ecotype had a reproductive trait that was relatively well-adapted to the local habitat type (see Supplement S3 for similar results on larger landscapes). In general, reproductive success was lowest in the majority LC habitat type near the boundary between the two habitat types, where individuals from HC would often disperse and win a territory, but subsequently suffer lowered reproduction due to being maladapted to LC.

The carryover effect led to the emergence of spatial genetic structure by habitat type (Fig. 2b), which in turn led to assortative mating. For example, in the HC habitat, the competitive exclusion of immigrants from LC meant that HC-adapted individuals were more likely to pair with other HC-adapted individuals. As a consequence, breeding pairs were more similar than random pairs with respect to both the reproductive genotype and, to a lesser extent, the neutral genotype (Supplement S4).

The degree of trait divergence depends upon both the relative frequencies of the habitats and the strength of the competitive advantage (c) conferred by HC (Fig. 3a,b, see also Fig. S2.1). We calculate trait divergence as the difference between the mean reproductive trait value in HC and LC. In the absence of a carryover effect, trait divergence occurs when the proportion of territories of different types is approximately equal ($c = 1$ in Fig. 3a,b). However, as the strength of the competitive advantage conferred by HC increases, trait divergence occurs at decreasing proportions of HC in the landscape ($c > 1$ in Fig. 3a,b). A deterministic version of the model confirmed this result (Supplement S2).

Trait divergence leads to evolution of habitat preference or insularity

All three dispersal traits evolved simultaneously with the reproductive trait, however they had different qualitative effects upon the stability and degree of local adaptation (Fig. 2c–e). Reproductive trait divergence was comparatively stable in time under the evolving NHPI scenario. In the evolving habitat preference scenario, intermittent loss of the HC-adapted ecotype was generally preceded by the LC subpopulation evolving habitat-type preferences for HC.

The coevolution of habitat preferences generally led to greater reproductive trait divergence (Fig. 3d,g) than the scenario where the reproductive trait evolves alone (Fig. 3b). Evolving habitat preference increased the range of landscape compositions for which trait divergence could occur, and strengthened the degree of divergence, particularly when the minority habitat type was small and the competitive advantage it conferred high. Evolving dispersal radius only strengthened trait divergence when the minority habitat type conferred a high competitive advantage and was rare; in this case, a smaller dispersal radius, or insularity, coevolved (Fig. 3j,k).

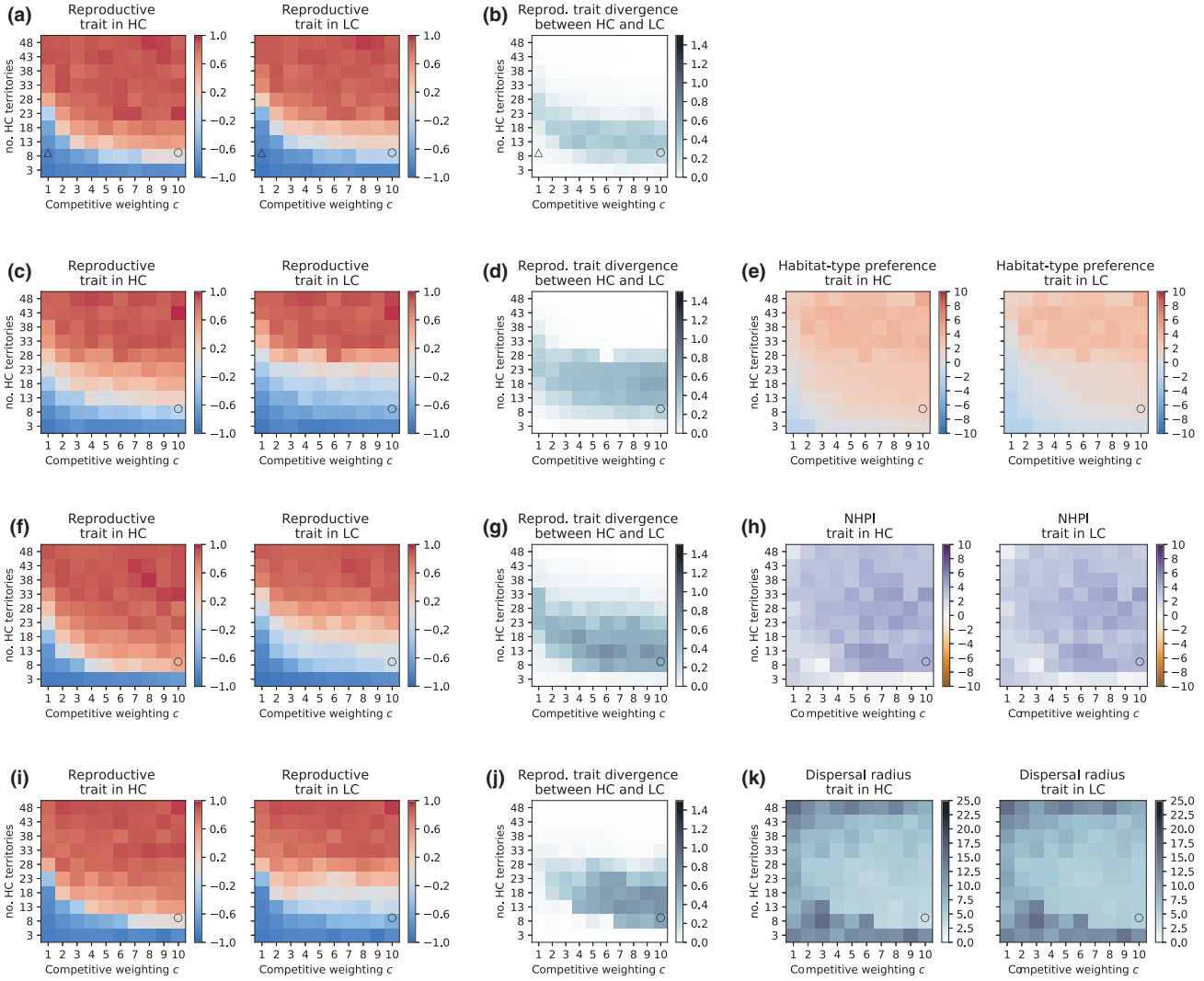

Figure 3 The effect of competitive weighting (c) vs. the number of territories conferring high competitive ability (HC) upon ecoevolutionary outcomes in the different habitat types. The evolutionary scenarios were evolving as follows: reproductive trait only (a–b), habitat-type preference (c–d), NHPI (f–h), and dispersal radius (i–k). Outcomes shown are mean reproductive trait in HC and LC (a,c,f,i), mean divergence in reproductive trait between HC and LC (b,d,g,j), and the mean dispersal trait in HC and LC (e,h,k). Dark areas in panels (b,d,g,j) show the region where trait divergence between habitats types occurs, leading to locally adapted ecotypes. Results are from simulations of the ecoevolutionary dynamics initialised with individuals with random genotype, run for 2000 generations, with means taken over the last 1500 generations. The triangle corresponds to the parameter values in Fig. 2a, and the circle corresponds to the parameter values in Fig. 2b–e. Default parameter values the same as in Fig. 2.

In all scenarios, the relationship between mean trait divergence and the parameters, landscape composition and competitive weighting, is noisy, reflecting the stochasticity inherent in the process. In general, increasing the mutation rate decreases the noise in the relationship between mean trait divergence and parameter values, and decreasing the number of loci determining each trait strengthens trait divergence (Supplement S5).

DISCUSSION

The key model findings were that: (1) local adaptation to a minority habitat can occur when the minority habitat type confers a competitive advantage to offspring as a carryover effect, and (2) dispersal traits that promote matching between ecotype and habitat type can coevolve with and strengthen local adaptation and trait divergence. We discuss each of these results in turn and then discuss the empirical evidence for the processes we have modelled.

Competitive carryover effect permits adaptation to high-quality minority habitat type

Both previous theory (Kawecki 1995) and our model predict that natural selection will favour adaptation to the majority habitat type; however, our model also predicts that, if the minority habitat type confers high competitive ability as a carryover effect, then adaptation to the minority habitat type can also occur, resulting in trait divergence. In the absence of carryover effects, the model predicts adaptation to the majority habitat type and ecological source–sink dynamics, and if dispersal characteristics can also coevolve then a preference to

disperse to the majority habitat type will favoured by selection. In contrast, in the scenario with competitive carryover effects, trait divergence can occur as a result of local adaptation to both the majority and to the high-quality minority habitat type.

Local adaptation occurs as a consequence of two factors. First, the carryover effect creates a competitive barrier to gene flow from the majority to the minority habitat, as the former produces individuals of low competitive ability (LC habitat) while the latter are of high competitive ability (HC habitat). Given that we model territory types that are clustered in space and dispersal from one location is not assumed to cover the entire global range, offspring raised in HC are more likely to settle in HC. These superior competitors in HC then act as a dispersal barrier to immigrants from LC, preventing immigrants from LC from winning the contest for breeding territories and reproducing in HC. Therefore, even though LC is the more frequent territory type, the competitive barrier prevents gene flow from LC to HC, and adaptation to the minority HC can occur.

The second factor is necessary to explain why HC individuals do not spread everywhere. Here swamping reduces the relative genetic contribution from the minority HC individuals to the majority habitat. Because LC territories are more frequent in the landscape, the relative contribution of genes in the other direction, from HC to LC, is low. Therefore, even though immigrants from HC are more likely to win a breeding territory in LC, the genes they carry that are locally adapted to HC are diluted by the preponderance of LC-types, and so adaptation to the majority LC is maintained.

Taking these two factors together, the population diverges into two ecotypes, one relatively specialised to HC and one to LC. Spatial genetic variation in the reproductive trait is by habitat type, and is maintained in the face of gene flow.

We propose that isolation by ecology may be initiated by carryover effects as described above. In current theory, isolation by ecology (Shafer & Wolf 2013) is initiated by divergent selection that is strong enough to counteract gene flow (Nosil 2007; Nosil *et al*. 2008). This creates a positive feedback in which local adaptation leads to a further reduction in realised gene flow between ecotypes (Rundle & Nosil 2005). In our model, the gene flow barrier is initiated by the effect of the environment upon the phenotype rather than as a genetic effect. Once trait divergence is initiated, reinforcement of the barrier may subsequently occur by mechanisms studied in the theory (reviewed in Richardson *et al*. 2014), such as lowered performance of immigrants (Nosil *et al*. 2005) or assortative mating via habitat preference (Benard & McCauley 2008).

Positive feedback between trait divergence and ecotype-habitat matching dispersal

Our model predicts a positive feedback between trait divergence and dispersal traits that match ecotype to habitat type, such as strong NHPI, small dispersal radius (insularity), or a match between reproductive trait and habitat-type preference. First, under trait divergence, individuals who preferentially disperse to habitat types that match their ecotype are more successful. Second, ecotype-habitat matching strengthens local adaptation and trait divergence, by increasing the proportion of time that a lineage spends in a particular habitat type, which reduces the need to adapt to the other type, and also by promoting assortative mating between individuals with similar habitat preferences, which reduces gene flow between ecotypes.

Trait divergence was more stable in time when individuals evolved to prefer their natal habitat type (NHPI) rather than a specific habitat *per se*, where the loss of trait divergence was generally preceded by HC-preference spreading to individuals in the LC habitat. We attribute this to differing effects that dispersal has on gene flow, i.e. how the respective habitat preference genes are expressed in a new habitat. Should an individual with a strong habitat-type preference disperse to its less preferred habitat, the consequence is more gene flow in the next generation (its offspring will 'desire' to disperse back); this effect on gene flow is absent in the NHPI scenario.

The evolution of ecotype-habitat matching dispersal traits is stronger if the high-quality habitat is rare, firstly because the smaller geographic size of the HC habitat means that the HC ecotype is under stronger selection against dispersal outside of its boundaries, but also because the smaller subpopulation size of the HC ecotype makes linkage disequilibrium more likely. Linkage disequilibrium manifests in the model as a correlation between the reproductive and dispersal trait; it arises spontaneously due to stochastic processes (c.f. Dieckmann & Doebeli 1999), which is more likely the smaller the population size (Gavrilets 2005), and creates a positive feedback with trait divergence. For example, in the evolving dispersal radius scenario, linkage disequilibrium will be most likely when HC is rare and therefore the HC subpopulation is small, and these are the conditions under which local adaptedness of the reproductive trait and a smaller dispersal radius coevolve (Fig. 3j,k). The role of linkage disequilibrium in the model can also be seen in the effect that reducing the number of loci has towards strengthening trait divergence (Fig. S5.1). The question remains whether the conditions that promote linkage disequilibrium in the model (high genetic variation, high mutation rates, few loci controlling traits, and low cost to habitat selectivity (Gavrilets 2005)) apply to real populations (reviewed in Bolnick & Fitzpatrick 2007). However, a condition for trait divergence – the rarity of high-quality habitat – is also a condition that promotes linkage disequilibrium.

In summary (Fig. 4), when the competitive advantage conferred by HC is high, trait divergence occurs when HC territories are rarer. Rarer HC territories promote the evolution of ecotype-habitat matching dispersal, both by strengthening selection on dispersal traits, and by making linkage disequilibrium more likely. Trait divergence and ecotype-habitat matching then enter a positive feedback, reinforcing one another, and this positive feedback both increases the range of landscape compositions for which trait divergence occurs and increases the degree of divergence.

Empirical relevance of the model

A potential empirical example: French-mainland vs. Corsican blue tits

Our prediction, that relative habitat qualities and frequencies can flip populations between ecological source–sink dynamics

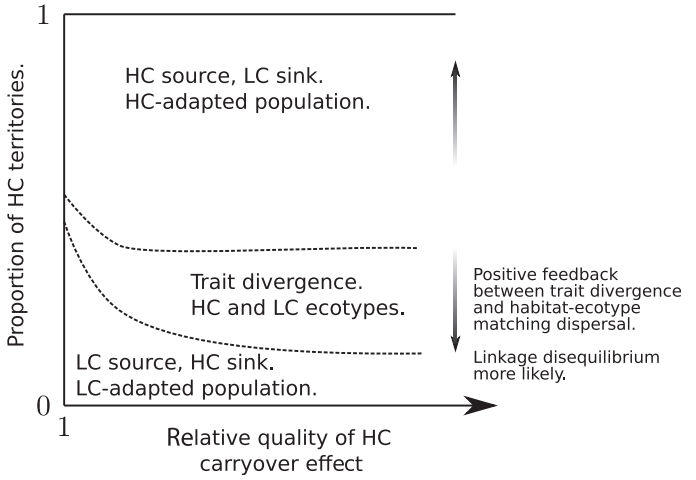

Figure 4 A conceptual diagram of the interaction between trait divergence, landscape composition, and habitat quality, showing the positive feedback mechanisms that enhance trait divergence when the minority habitat type has high quality and is rarer in the landscape.

and local adaptation, appears to fit quite well with studies of blue tits (*Cyanistes caeruleus caeruleus*) in France. On the mainland, the majority habitat type is deciduous, and blue tits who settle in the rarer evergreen patches are maladapted (Blondel *et al*. 1993), resulting in source–sink dynamics (Dias & Blondel 1996; Dias *et al*. 1996). On Corsica, however (subspecies *C. c. ogliastrae*), where evergreen habitat dominates, the source–sink pattern is not simply reversed. Instead, trait divergence into two ecotypes has been documented, with genetic variation being structured by habitat type (Porlier *et al*. 2012). The two ecotypes differ in a number of heritable or partially-heritable traits (reviewed in Charmantier *et al*. 2016), and the differences are maintained despite spatial proximity (Lambrechts *et al*. 1997; Blondel *et al*. 1999).

Trait divergence in our model requires that the minority habitat, deciduous in the case of Corsica, confer a competitive advantage attributable to phenotypic changes that result from being raised there. Indeed, the deciduous habitat has higher quality (Lambrechts *et al*. 2004) and the deciduous ecotype is socially dominant over the evergreen ecotype in a number of ways. The deciduous ecotype is bigger than the evergreen ecotype, which is partially attributable to the habitat's relative resource richness (Braillet *et al*. 2002). Habitat richness may also contribute to the stronger coloration, suggestive of social dominance, of the deciduous ecotype (reviewed in Charmantier *et al*. 2016). Finally, caterpillar phenology is one month earlier in the deciduous habitat (Blondel *et al*. 1999), which permits earlier production of offspring so they can obtain a prior residence advantage (Braddock 1949; Kokko *et al*. 2006) over territory before immigrants can arrive (Braillet *et al*. 2002). Further, blue tits display ecotype-matching habitat preferences (reviewed in Charmantier *et al*. 2016), and Corsican blue tits are insular with lower dispersal distance (Blondel *et al*. 1999; Blondel 2000), which is also predicted by our model.

If trait divergence on Corsica were initiated by carryover effects upon competitive ability, it may have been subsequently reinforced by mechanisms that also maintain it today. For example, the heritable difference in laying date (Caro *et al*. 2007) may be reinforced (Charmantier *et al*. 2016) by assortative mating by allochrony (Hendry & Day 2005). As another example, larger body size results from a richer habitat, but it also has significant heritability (Charmantier *et al*. 2004), and selection differs by habitat type (Teplitsky *et al*. 2014), therefore some migration barriers that were a pure carryover effect in the past may now be strengthened as a genetic difference between ecotypes today.

Empirical support for model components

Empirical support for separate components of the model can be found in a wide range of taxa, and we list some examples of partial support (see Table 2). The key components of the model are: (1) a carryover effect initiated by natal habitat type that (2) influences the offspring's ability, as an adult, to compete for breeding resources, in a way that (3) promotes a lineage's likelihood of finding itself in a high-quality habitat-type. The relative abundance of high-quality habitat will then determine the ecoevolutionary outcome, i.e. either local adaptation or source–sink dynamics.

Regarding component (1), carryover effects are commonly documented to be initiated by the natal habitat type (Lindström 1999; Van Allen & Rudolf 2016). This includes examples where component (2) is key, i.e. the carryover effects manifest as a competitive advantage at the adult stage. For example, juvenile winter-resident birds often have a higher social rank if they have joined the winter flock earlier, which increases their probability of winning the area as their breeding territory (e.g. Saitou 1979; Hogstad 1987; Nilsson & Smith 1988; Ekman 1989; Matthysen 1990; Sandell & Smith 1991; Koivula *et al*. 1993). Joining time is constrained by breeding time, which in turn depends upon resource phenology in the natal habitat (Johansson *et al*. 2014, 2015), therefore habitat patches with earlier resource phenology may provide a competitive advantage. Prior residence effects, in general, have been observed in a wide range of taxa, including insects (e.g. Waage 1988; Takeuchi & Honda 2009), amphibians (e.g. Mathis *et al*. 2000), crustaceans (e.g. Peeke *et al*. 1995) and mammals (Haley 1994).

Natal habitat richness is a common example; larvae of the burying beetle (*Nicrophorus vespilloides*) who were raised in a highly nutritious environment obtained larger adult size, and larger relative size is often advantageous in contests for breeding resources (Hopwood *et al*. 2014). Natal nutrition can also influence the development of sexual characteristics relevant to competition for territory and mates, e.g. via the brighter plumage (e.g. Wilkin & Sheldon 2009; Evans & Sheldon 2011) or better singing (e.g. Spencer *et al*. 2004; Grava *et al*. 2012) of male birds raised in high-quality territories.

As a final example, in the snow buttercup (*Ranunculus adoneus*), early-snow-melting sites have a longer growing season and thus produced higher quality seeds. The asymmetric gene flow from early-melting to late-melting sites was found to have a homogenising effect; it was strong enough to counteract the localised adaptation that would have otherwise been expected given the large difference in flowering phenology between sites (Stanton *et al*. 1997).

Table 2 Empirical examples of components of the model

Species and reference	Carryover effect initiated by natal habitat type	Carryover influences competition	Repetition of lineage in high-quality habitat
Snow buttercup (*Ranunculus adoneus*) Stanton *et al*. (1997)	Early snowmelt sites have longer growing season, produce higher quality seeds	Higher-quality seeds have greater emergence and early survival	Early snowmelt sites demonstrated to be genetic source
Oystercatchers (*Haematopus ostralegus*) (Van Treuren *et al*. 1999; Van De Pol *et al*. 2006; Ens *et al*. 2014)	Territory nearer feeding area leads to higher body mass (corrected for size)	Unknown: while habitat influenced mass, it was instead size that determined recruitment (due to fighting ability?)	Individuals reared in high-quality habitat had higher probability to recruit to same, no genetic division between habitat types
Black-capped chickadees (*Poecile atricapillus*) (Grava et al., 2012, 2013a)	Mature forests with greater food resources during development phase of song-learning leads to dominant-male song type	Dominant-male song type increases territoriality, ability to attract female	Could explain why adult males occupying territory in mature forest had dominant-male song type
Great tits (*Parus major*) (Wilkin & Sheldon 2009)	Larger natal territory at lower altitudes (advances birth date) improved male lifespan and breeding success regardless of subsequent breeding environment	Considered plausible that competitive advantage (e.g. via brighter plumage) was responsible	Not shown; females preferred high-quality territory but carryover effect on females not detected
Great tits (*Parus major*) (Verhulst *et al*. 1997)	Birds raised in high-quality habitat have higher mass as nestling	Not shown but larger individuals known to be socially dominant so competition proposed as mechanism	Not shown directly, though only larger birds from the low-quality habitat could disperse into the high-quality habitat
Rock pigeons (*Columba livia*) (Hsu *et al*. 2017)	Experimentally lowered food quality and quantity post-hatching reduced mass, postural male display, female attractiveness, pairbonding, and male aggression as adults	Not shown but size important to male-male competition, and life-long pair-bond means lowered female attractiveness very likely important	Not studied
Burying beetles (*Nicrophorus vespilloides*) (Hopwood *et al*. 2014)	Larger mouse carcass increases size as adult	Adult size increases probability to win mate and carcass as adult	Not studied
Zebra finches (*Taeniopygia guttata*) (Spencer & Verhulst 2007)	Experimental exposure to stress hormone during nestling phase depressed growth, increased neophobia, and reduced social dominance	Test was for competition for a perch not breeding resource	Not studied

The above examples clearly differ in the likelihood of informed dispersal, however in our context it is sufficient that the species has some mechanism promoting the repeated presence of a lineage in a specific habitat type (component 3 envisaged above). One mechanism we expect to be common is a spatial structure such that adjacent habitats are more likely to be of a similar type (as assumed in our model), but we are particularly interested in a causal route where the high quality of a habitat itself causes individuals originating there to have a greater chance, as adults, to be competitive enough to breed there (i.e. silver spoon competition hypothesis Stamps 2006) Empirical examples include territory-holding male black-capped chickadees (*Poecile atricapillus*), who demonstrated a positive relationship between habitat quality and song quality (Grava *et al*. 2012, 2013a,b), which can aid in territory acquisition and maybe more commonly in mate acquisition. As a second example, oystercatchers (*Haematopus ostralegus*) raised on high-quality territories had a higher probability of settling in and breeding on another high-quality territory compared to those raised in low-quality territories (44% vs. 6%) (Van De Pol *et al*. 2006; Ens *et al*. 2014).

It is also worth commenting on carryover effects across multiple habitats and life stages. Migratory birds can encounter competition for wintering sites before eventually competing for breeding territories, and there is some evidence linking condition and territory-quality at each stage to previous stages and back to natal conditions. For example, the Icelandic black-tailed godwit (*Limosa limosa islandica*) shows a correlation between hatching date and subsequent first arrival date to the breeding grounds (Gill *et al*. 2014). Other studies have established causality over a single migratory stage of the species in question. Hatching earlier or in a higher quality breeding territory can lead to a better quality winter territory, because of juvenile condition, more time to sample better locations, or prior residence effects (Marra 2000; Gunnarsson *et al*. 2005; Snell-Rood & Cristol 2005; Sergio *et al*. 2007; Johnson *et al*. 2009; Meller *et al*. 2013). In the second stage, a better quality winter territory can lead to a better quality breeding territory (Norris *et al*. 2004), because of energetic carryover effects (Alves *et al*. 2013; Catry *et al*. 2013), earlier arrival (Studds & Marra 2005), or if better quality wintering sites are geographically closer to the breeding sites (Hötker 2003; Bearhop *et al*. 2004; Norris *et al*. 2004; Bregnballe *et al*. 2006). For long-lived species, the first pass through the migratory cycle must continue to influence an individual over its lifetime, such as if adults maintain relative timing throughout annual cycle (Tøttrup *et al*.

2012) or due to high winter-site tenacity (Wunderle Jr & Latta, 2000; Burton & Armitage 2008; Alves *et al*. 2013).

There are many types of carryover effects apart from those we modelled. Changes to survival instead of competitive ability are commonly reported (e.g. Reid *et al*. 2006; Kavanagh *et al*. 2010), which we expect to affect local adaptation in a similar way to per-capita growth rates in source–sink models (Holt & Gaines 1992). High-quality offspring may instead travel further and persist longer in the search for a high-quality breeding resource (search hypothesis Stamps 2006). We expect this to have a similar outcome to our model, potentially removing the need for similar habitat to be clustered in space as we assumed; however, settlement decisions will interact with landscape-composition information obtained during the search (Davis 2007), so a model may be needed to disentangle effects. Adaptive developmental effects that instead anticipate a similar adult environment (e.g. Dantzer *et al*. 2013) will give no necessary advantage to offspring travelling from high- to low-quality habitat but reduce gene flow in both directions. With temporally varying environmental conditions shared across habitats, offspring from low-quality territories may have higher performance in poor years (c.f. Douhard *et al*. 2014), which we expect to erode trait divergence in our model. Finally we note that negative carryover effects may be ameliorated by later developmental trade-offs, for example compensatory growth at the cost of lower survival probability (reviewed in Metcalfe & Monaghan 2001), or sexual attractiveness traded against senescence (Blount *et al*. 2003), therefore the effect in our model depends upon the constraints on such trade-offs.

In summary, we have highlighted a potentially strong divergence-promoting force for which there is tantalising partial empirical support. There is probably nothing unique about the one empirical example in the literature that provides support for all components of our model, since various components of the mechanisms underlying our model are reported in a wide range of taxa. Carryover effects that combine with habitats differing in both the quality and quantity of offspring produced can potentially lead to reductions in gene flow, with clear consequences for biological diversity.

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AUTHORSHIP

NPK, JJ and HGS conceived the initial research direction; NPK and HK refined concepts and conceived approach; NPK created and analysed all models; NPK and HK wrote the manuscript; JJ commented on the manuscript and models; RAC critiqued the models and provided material support; HK obtained funding.

DATA ACCESSIBILITY STATEMENT

Code for the model is available for download from the Github repository archived DOI: https://doi.org/10.5281/zenodo.1249073

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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